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REIDENTIFICATION OF LATE MIDDLE EOCENE “*UINTACYON*” FROM THE GALISTEO FORMATION (NEW MEXICO, U.S.A.) AS AN EARLY BEARDOG (MAMMALIA, CARNIVORA, AMPHICYONIDAE)

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ABSTRACT. Museum of Comparative Zoology (MCZ) VPM-4225, a carnivoran dentary, is described here for the first time, 82 years after it was collected in the Duchesnean (late middle Eocene) portion of the Galisteo Formation in New Mexico. It evidently corresponds to the specimen—never identified by its catalog number, never described, and considered missing for the last 41 years—that formed the basis for the purported occurrence of the early carnivoraform *Uintacyon* in the formation reported in 1943. The specimen is here reidentified as one of the earliest amphicyonids, *Angelarctocyon*, which was previously known from only two specimens from the Chambers Tuff of Texas. With this reidentification, there is no longer a valid occurrence of *Uintacyon* postdating the Uintan North American Land Mammal Age, adding to the evidence for rapid replacement of ancient carnivoramorph lineages by early crown-clade carnivorans in the late middle Eocene, across a period of severe climatic fluctuations 42–40 million years ago.

KEY WORDS: Duchesnean; Galisteo Formation; Amphicyonidae; Tonque local fauna

INTRODUCTION

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The Duchesnean North American Land Mammal Age (NALMA), ca. 41–38 million years ago (Ma; Kelly et al., 2012), marks a pivotal early stage of the Eocene–Oligocene terrestrial faunal transition in North America (Prothero, 1994; Rasmussen et al., 1999; Robinson et al., 2004; Figueirido et al., 2012). It is also an important period for understanding the demise of early carnivoraform lineages (i.e., close relatives of carnivorans) and the rise of crown-group carnivorans (cf. Tomiya, 2011; Tomiya and

Tseng, 2016). Although a diverse array of carnivorous mammals is known from Duchesnean-age deposits of what is now the southwestern U.S.A., many of them are represented by few specimens (Gustafson, 1986; Tomiya, 2013). As such, careful documentation of all available materials is essential for clarifying the patterns of Duchesnean carnivore diversity in time and space. The purpose of this paper is to document a hitherto uncited and undescribed specimen that evidently formed the basis for an occurrence of the carnivoraform *Uintacyon* in the Duchesnean portion of the Galisteo Formation of New Mexico (Stearns, 1943). If that previous taxonomic identification were correct, this specimen would represent the last surviving member of the oldest known carnivoraform genus (cf. Solé et al., 2016). However, on the basis of a close inspection of the dental morphology, we identify it instead as one of the earliest amphicyonid carnivorans, or the “beardogs.”

METHODS

Anatomical terminology follows primarily Tomiya and Tseng (2016) and in part Van Valen (1966). We tentatively accept Carnivoraformes and Carnivoramorpha (the latter consisting of viverravids and carnivoraforms) as successively more inclusive laurasiatherian clades that include crown-group Carnivora (Flynn et al., 2010), while recognizing the need for additional testing of the hypothesized monophyly of Carnivoramorpha (cf. Zack, 2019). Measurements were taken with digital calipers to the nearest 0.01 mm.

Institutional Abbreviations. CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts,

U.S.A.; TMM, Texas Memorial Museum (in collection of the Vertebrate Paleontology Laboratory, University of Texas at Austin), Austin, Texas, U.S.A.

RESULTS

Systematic paleontology

Class Mammalia *sensu* Rowe, 1988;
unranked clade Carnivoraformes Flynn,
Finarelli, and Spaulding, 2010
Order Carnivora *sensu* Bryant, 1996;
unranked clade Caniformia *sensu* Bryant,
1996
Family Amphicyonidae Trouessart, 1885
Genus *Angelarctocyon* Tomiya and Tseng,
2016

Angelarctocyon cf. *A. australis* (Gustafson)
Tomiya and Tseng, 2016

Uintacyon sp. Stearns, 1943, p. 310

Uintacyon sp. Lucas and Kues, 1979, p. 227

Carnivora indet. Lucas, 1982, p. 18

Uintacyon sp. (in part) Flynn, 1998, p. 119

Referred Material. MCZ VPM-4225, right partial dentary with p2-m1 and alveoli for c1, p1, and m2-3.

Locality and Horizon. Sweet’s Ranch, “east of Los Cerrillos” (Stearns, 1943:310), Santa Fe County, New Mexico, U.S.A. (“T” in Fig. 1). “[A] sandstone probably less than 200 feet below the Espinazo volcanics [= Espinazo Formation]” (Stearns, 1943:310), upper portion of Galisteo Formation corresponding to Duchesnean NALMA (Lucas, 1982).

Description. The referred dentary is missing a small portion of its anterior extremity, most of the coronoid process, and part of the articular surface of the mandibular condyle (Fig. 2). In addition, the ventrolateral portion of its horizontal ramus appears to have been damaged and is augmented with plaster. As such, the positions of mental

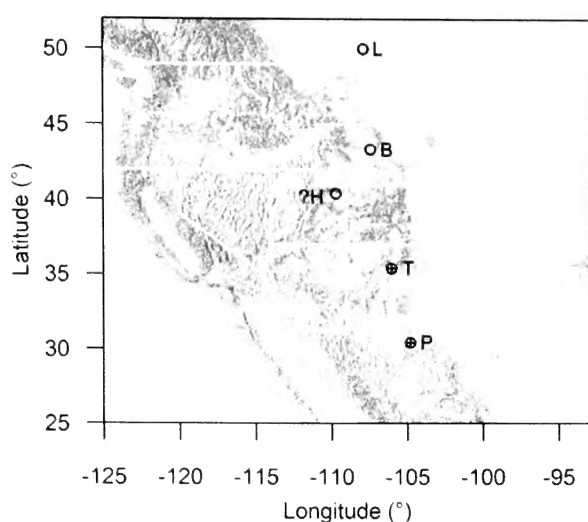


Figure 1. Occurrences of Duchesnean amphicyonids in North America (crossed circles for *Angelarctocyon*). Abbreviations: B, Badwater Creek area (Wagon Bed Formation, Wyoming); L, Lac Pelletier lower fauna (Cypress Hills Formation, Saskatchewan, Canada); P, Porvenir local fauna (Chambers Tuff, Texas); T, Tonque local fauna (Galisteo Formation, New Mexico); ?H, Halfway Hollow area (Duchesne River Formation, Utah; possible *Brachyrhynchocyon*). See Table 3. Relief map from U.S. Geological Survey National Center for EROS (2005).

foramina are unknown. The dentary is rather gracile and exhibits gradual, rather than abrupt, tapering toward its anterior end. The posterior border of the mandibular symphysis is at the same anteroposterior level as the anterior border of p2. The shallow slope of the anterior base of the coronoid process is suggestive of a relatively low coronoid process compared with other early caniform carnivorans such as *Lycophocyon hutchisoni* and *Hesperocyon gregarius* (Wang, 1994; Tomiya, 2011). The preserved portion of the masseteric fossa is anteriorly clearly delineated by a crest but is otherwise shallow, owing to the gracile construction of the ascending ramus. The angular process, which appears to be completely preserved, is modest in size and not as elongate as in *L. hutchisoni*. The mandibular condyle is also

slender, befitting the overall form of the element.

The lower teeth generally show little wear. Small diastemata separate the alveoli for c1, p1, and p2. The p2 is similarly proportioned to the slightly larger p3, although the bulging of anterior and posterior cingulids is further reduced. Compared with the holotype of *Angelarctocyon australis*, FMNH PM 423, p3 and p4 of MCZ VPM-4225 are somewhat more anteroposteriorly compressed (such that the main cuspids appear proportionately taller) and bear better-developed anterior and posterior cingulids. Specifically, the anterior cingulid of p4 and the posterior cingulids of p3 and p4 are sufficiently developed to retain short longitudinal ridges (pbr in Fig. 2D), and the labial border of posterior cingulid of p4 is delineated by a sharp edge, unlike in FMNH PM 423. The main cuspid of p3 clearly lacks an accessory cuspid on its posterior slope, as has been suggested for *A. australis* on the basis of the damaged right p3 of FMNH PM 423 (Tomiya and Tseng, 2016). The dorsally positioned posterior accessory cuspid of p4 (pac in Fig. 2) has a steplike profile with a steeply descending posterior slope; this trait is a synapomorphy of the family Amphicyonidae (Tomiya and Tseng, 2016).

The m1 bears a trigonid that is somewhat more closed (i.e., the prevallid and postvallid are less divergent) in occlusal view than that of FMNH PM 423 because the paracristid is more lingually directed. The anterolabial cingulid is weakly developed. The moderately large talonid bears a broad, concave basin that is approximately as wide as it is long. As in FMNH PM 423, the apex of m1 hypoconid in MCZ VPM-4225 is positioned close to the labial edge of the talonid, although the anterior portion of the cristid obliqua is slightly more lingually directed than in the holotype. A small sharp notch marks the anterior terminus of the cristid

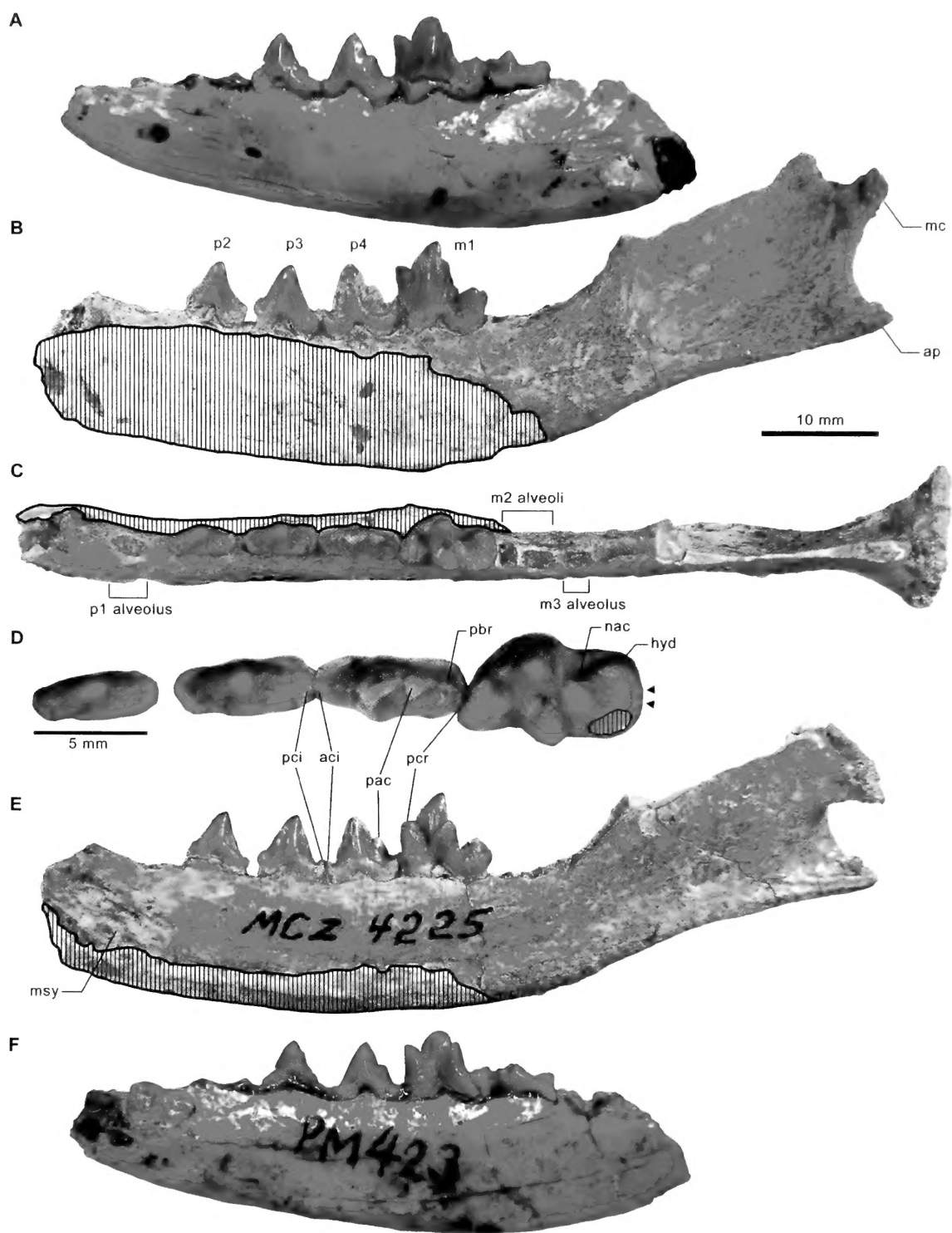


Figure 2. Dentaries of *Angelarctocyon*. A, F, right partial dentary of FMNH PM 423 (holotype of *A. australis*) in lateral (A; inverted) and medial (F) views. B–E, right partial dentary of MCZ VPM-4225 (*Angelarctocyon* cf. *A. australis*) in lateral (B; inverted), occlusal (C; close-up of teeth in D), and medial (E) views. In D, hatched area indicates breakage on entoconid, and black triangles point to minor cuspidulids along posterior margin of talonid basin. Same 10-mm scale bar applies to A–C, E, F. Images in B–E courtesy of Museum of Comparative Zoology, Harvard University (©President and Fellows of Harvard College). Abbreviations: aci, anterior cingulid; ap, angular process; hyd, hypoconid; mc, mandibular condyle; msy, mandibular symphysis; nac, notch anterior to cristid obliqua; pac, posterior accessory cuspidulid; pbr, posterior basal ridge; pci, posterior cingulid; pcr, paracristid.

TABLE 1. MEASUREMENTS (MM) OF MCZ VPM-4225 (*Angelarctocyon* cf. *A. australis*).

	p2	p3	p4	m1	m1 Trigonid	m2	m3	Dentary
L ^a	5.09	5.91	6.76	8.28	5.20	4.54 ^b	2.23 ^b	~72.1 ^c
W	1.97	2.50	2.84	4.55				

^aAbbreviations: L, anteroposterior length; W, labiolingual width.
^bAlveolar length.
^cMeasured from anterior border of c1 alveolus to mandibular condyle.

obliqua—a feature that may have been obliterated by wear in FMNH PM 423. Faint cuspidals are present on the posterior border of the talonid basin (indicated by triangles in Fig. 2D). The m1 entoconid, which is subequal in height to the hypoconid in FMNH PM 423 (Tomiya and Tseng, 2016), appears to be largely broken off in MCZ VPM-4225. A moderately large m2 (having roughly two-thirds of the length of m1) with an anteroposteriorly compressed trigonid is indicated by its alveoli. The single-rooted m3 appears to have been about half as long as m2 (Table 1).

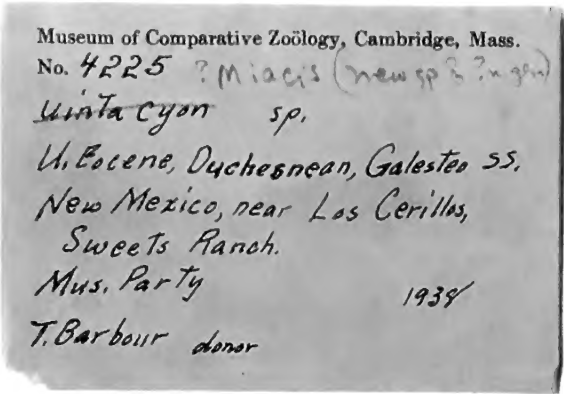
DISCUSSION

MCZ VPM-4225 was previously identified on the specimen label (Fig. 3A) and in the MCZ collections database (as of 20 September 2017) as the noncarnivoran carnivora-form *Uintacyon*. However, it clearly differs from *Uintacyon* in having: (1) a slender dentary that tapers more gradually toward its anterior end; (2) labiolingually more compressed lower premolars of less disparate sizes (in contrast to the much smaller sizes of p2 and p3 relative to p4 in *Uintacyon*); (3) a more dorsally positioned posterior accessory cuspidal on p4; (4) a relatively longer m1 trigonid, in which the prevallid is appreciably longer than the postvallid; and (5) a labiolingually broader m1 talonid and talonid basin (the talonid basin is typically only about half as wide as the trigonid in *Uintacyon*). It further differs from middle Eocene species of *Uintacyon* in having a

more concave m1 talonid basin and likely an m2 with a more anteroposteriorly compressed trigonid (based on the shape of the anterior alveolus). Instead, this carnivora-form most closely resembles the early amphicyonid carnivoran *A. australis*, which thus far is known from just two specimens (a set of jaws and a dentary fragment with m2) from the lower portion of Chambers Tuff in Texas (Gustafson, 1986; Tomiya and Tseng, 2016).

Indeed, the specimen from New Mexico exhibits all the differentially diagnostic traits of *Angelarctocyon* so far as the lower dentition is concerned (Tomiya and Tseng, 2016). In comparison with other small Eocene amphicyonids, it differs from: (1) *Daphoenus lambei* in being >30% smaller (in m1 anteroposterior length; cf. Hunt, 1996); (2) *Daphoenus demilo* (which may be conspecific with *D. lambei*; Hunt, 1996) in having a posteriorly more gracile dentary (dentary depth below m1 is roughly 150% of the height of m1 compared with ~200% in the holotype CM 15596; Dawson, 1980: fig. 2), relatively taller lower premolars, and a single-rooted m3 (double-rooted in CM 15596); (3) *Cynodictis lacustris* (genotypic species of *Cynodictis*) in having less robust premolars and a less open m1 trigonid. Direct comparison with the Chadronian *Gustafsonia cognita* is not possible, as it is known only from the holotype cranium, but the linear dimensions of the teeth of MCZ VPM-4225 are roughly 20% larger than expected for the holotype of *G. cognita*.

A



B

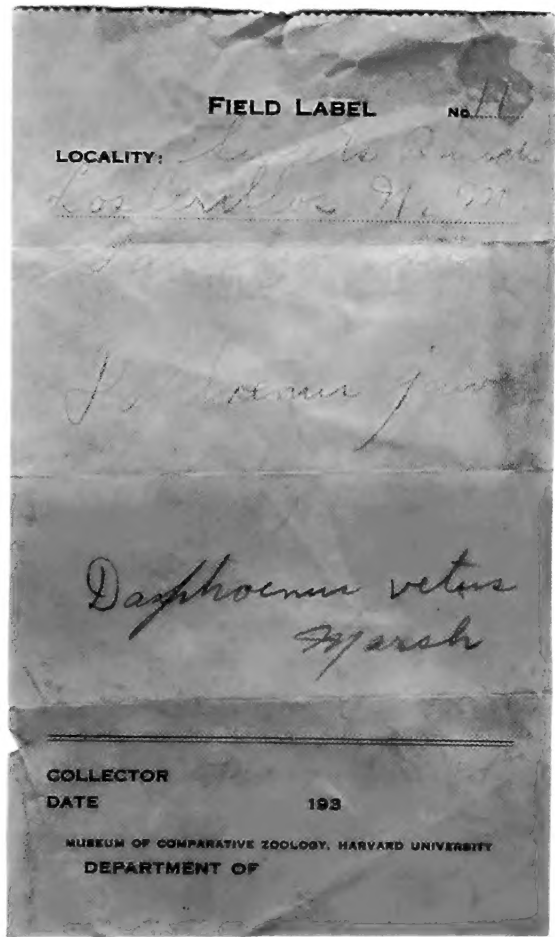


Figure 3. Specimen label (A) and field label (B) for MCZ VPM-4225 (color and contrast were digitally modified to enhance legibility). Courtesy of Museum of Comparative Zoology, Harvard University (©President and Fellows of Harvard College).

TMM 40209-200, whereas they closely match those of *A. australis* (cf. Gustafson, 1986).

Although the specimen is here confidently referred to the currently monospecific genus *Angelarctocyon*, its species-level referral to *A. australis* is tentative considering the dental morphological differences from FMNH PM 423 as described above. These differences, although subtle, are all suggestive of more plesiomorphic conditions, which are consistent with the potentially older geologic age of MCZ VPM-4225 (see below). Alternatively, these minor differences could be ascribed to geographic variations over a potentially biogeographically significant distance (~600 km at present) that separated the New Mexico locality from the holotype locality of *A. australis* in Texas. In any case, a close affinity between MCZ VPM-4225 and FMNH PM 423 is indubitable, and it would be premature to propose a separate species on the basis of the very limited data at hand.

The specimen metadata preserved at MCZ, combined with information in the published literature, help illuminate the long-obscure history of MCZ VPM-4225 (Table 2), which we reconstruct as follows (see below for justification). In the summer of 1938, Theodore E. White, then a research associate working with Alfred S. Romer at MCZ (Lyman, 2016), conducted fieldwork at Sweet's Ranch near Los Cerrillos, New Mexico and collected the specimen (Stearns, 1943). It was recorded as a "*Daphoenus jaw*" on the field label and later updated as *Daphoenus vetus* (Fig. 3B). It is not entirely certain whether these identifications were made by White himself, who also listed it as "*Cynodictus*" [sic] in his field notes (Lucas, 1982). The latter identification may have been referring to the Eurasian amphicyonid *Cynodictis* or the North American canid *Hesperocyon* (which was sometimes classified as *Cynodictis*; cf. Wang, 1994). Then, on the

TABLE 2. SYNOPSIS HISTORY OF MCZ VPM-4225.

Year	Event	Sources	Remarks
1938	Collected by T. White. Identified (by White?) as <i>Daphoenus</i> (later <i>Daphoenus vetus</i>) on field label. Identified as “ <i>Cynodictus</i> ” [= <i>Cynodictis</i>] in T. White’s field notes.	Stearns (1943); field label (Fig. 3B); T. White’s field notes cited in Lucas (1982)	Year of collecting is not 1939 as reported by Stearns (1943:310).
1943	Reported as <i>Uintacyon</i> sp. without specimen citation, description, or a figure.	Stearns (1943)	Identification by T. White.
1955–1962?	At MCZ: Considered (unpub.) a possible procyonid relative.	B. Patterson notes (undated) stored with specimen	Patterson disagrees with identification as <i>Uintacyon</i> .
1962–1963	At MCZ: Considered (unpub.) a new genus and a new species related to <i>Miacis</i> .	G. MacIntyre notes (1962–1963) stored with specimen	MacIntyre apparently intended to name a new taxon after Patterson.
1979	Specimen remains uncited and undescribed; not found in MCZ and considered possibly lost.	Lucas and Kues (1979)	
1982	White’s field notes listing <i>Cynodictus</i> from Galisteo are discovered and thought to be in reference to Stearns’ (1943) <i>Uintacyon</i> sp. Specimen not found in MCZ. <i>Uintacyon</i> removed from Tonque local faunal list (Lucas, 1982).	Lucas (1982)	
2020	Described and reidentified as amphicyonid <i>Angelarctocyon</i> .	This paper	

basis of this specimen, Stearns (1943:310) reported an occurrence of “*Uintacyon* sp.” at Sweet’s Ranch, attributing that taxonomic identification to White. Stearns did not, however, cite or describe the voucher specimen for this purported occurrence. In reviewing the vertebrate fossil assemblages from the Galisteo Formation, Lucas and Kues (1979) were unable to locate the pertinent material at MCZ and suggested that the specimen might have been lost. Subsequently, Lucas (1982:18) discovered the 1938 field notes of White at MCZ and determined that the jaw of *Cynodictus* [sic] listed in them likely corresponded to *Uintacyon* sp. of Stearns (1943). Still, the specimen itself was nowhere to be found, and in consultation with the then-MCZ curatorial associate Charles Schaff, he concluded that “it never was entered into the MCZ collec-

tion” (Lucas, 1982:19). Being unable to confirm the identity of *Uintacyon*, Lucas (1982) listed it as an indeterminate carnivoran in his faunal list for the upper portion of the Galisteo Formation (Tonque local fauna).
Here, MCZ VPM-4225 is cited for the first time as the basis for the occurrence of *Uintacyon* reported by Stearns (1943). Even though the presumed original specimen label (Fig. 3A) lists the year of collection as 1938, not 1939 as noted by Stearns (1943:310), there is little doubt about their correspondence because, as far as we are aware, it is the only MCZ specimen from Sweet’s Ranch that was at one point identified on its specimen label as *Uintacyon*. In fact, it is the only carnivoramorphan specimen from Sweet’s Ranch in the MCZ collections catalog. Furthermore, one of us (ZSM)

searched the MCZ archive but did not find field notes or records by White from any trip in 1939 to Sweet's Ranch. Therefore, it is unlikely that he collected there in 1939, and Stearns (1943) must have incorrectly reported the collecting year, as suspected by Lucas (1982). We are also confident in linking this specimen to *Cynodictus* [sic] from Sweet's Ranch mentioned in White's unpublished 1938 field notes (cf. Lucas, 1982) because it is the only carnivore he lists, and the dentary of MCZ VPM-4225 matches the description as a jaw.

The relatively primitive morphology of *Angelarctocyon* compared with better-known later amphicyonids has generated much confusion and delayed its recognition as one of the earliest beardedogs (Tomiya and Tseng, 2016). MCZ VPM-4225 appears to have undergone the same fate. At least five different taxonomic identities—including as a relative of procyonids and an undescribed species of the early carnivoramorph *Miacis*—have been suggested for this specimen since its discovery 82 years ago (Table 2). In retrospect, it is interesting that the initial, never-published identification as either *Daphoenus* or *Cynodictis* (assuming that the latter referred to the Eurasian amphicyonid and not *Hesperocyon*) proved to be the most perspicacious. It should be noted that the recognition of *A. australis* as an amphicyonid benefited from: (1) the preservation of several upper teeth in the holotype, which was collected in 1946 but remained undescribed for 40 years (Gustafson, 1986); and (2) computed-tomographic data on the internal cranial morphology of its close relative, *G. cognita* (Tomiya and Tseng, 2016). Without a web of such information, accurate family-level classification of an isolated dentary like MCZ VPM-4225 had to be difficult.

MCZ VPM-4225 represents one of the earliest records of the family Amphicyoni-

dae. Prothero and Lucas (1996) correlated an upper portion of the Galisteo Formation in the vicinity of Los Cerrillos, which had yielded elements of the Tonque local fauna, with Chrons C18n.1n to C17n.3n (39.55–37.92 Ma; Kelly et al., 2012). Thus, MCZ VPM-4225 is potentially older than the holotype FMNH PM 423 of *A. australis* (from a portion of the Chambers Tuff, Texas, which was correlated with C17n.3n by Kelly et al. [2012]) by as much as ~1.6 million years. If future work shows the Tonque local fauna to be indeed older than the Porvenir local fauna, it will make *Angelarctocyon* the second-oldest amphicyonid genus after *Daphoenus*, which first appears at the early-Duchesnean Locality 20 in the Badwater Creek area, Wyoming (Dawson, 1980; Hunt, 1996).

The rediscovery of Stearns' *Uintacyon* is significant because if MCZ VPM-4225 actually belonged to *Uintacyon*, it would represent the last known—and the only post-Uintan—occurrence of the genus (cf. Flynn, 1998). With our reidentification of this specimen, the last occurrence of *Uintacyon* is pushed back to the Uintan NALMA and is represented by the holotype YPM VP 013101 of *Uintacyon acutus* from the Uinta Formation of Utah (Thorpe, 1923). This last appearance date happens to agree with the temporal range of the genus reported by Heinrich et al. (2008), although *U. acutus* was not included in their list of species. The timing of the demise of *Uintacyon*, which first appeared in the late Paleocene (Gingerich, 1983), accentuates the pattern of almost complete genus-level replacement of early-diverging carnivoraforms by crown-group carnivorans between the late Uintan and Duchesnean NALMAs (Table 3; see Tomiya [2011], Solé et al. [2014], and Tomiya and Tseng [2016] for phylogenetic hypotheses). This transition apparently coincided with major climatic fluctuations between

Table 3. Distributions of carnivoraforms from late Uintan (Ui3 subage) to Duchesnean of North America

	Ui3	latest Uintan earliest Duchesnean	Duchesnean
<i>Miocyon scotti</i>	[Utah] ^d		
<i>Miocyon vallisrubrae</i>	Tex. ^{b,c}		
<i>Miocyon</i> sp.	Calif. ^{d,e} , Tex. (cf.) ^{b,i} , Wyo. ^{c,g,h} , Sask. ^{c,h,i}	Calif. ^c	?Utah ^{b,i}
<i>Miocyon magnus</i>			Sask. ^h
<i>Tapocyon robustus</i>	Calif. ^{k,l} , Utah ^{e,m} , Wyo. (cf.) ⁿ	Calif. ^c	
<i>Tapocyon dawsonae</i>	Calif. ^l		
<i>Tapocyon</i> sp.	[Mont.] ^o		
<i>Procyonictis vulpiceps</i>	Tex. (cf.) ^l , [Utah] ⁱ		
<i>Procyonictis progressus</i>	Calif. ^{d,e,p}		
<i>Procyonictis</i> sp.	Wyo. ^g		
“ <i>Miacis</i> ” <i>gracilis</i>	Calif. (cf.) ^e , Utah ^q		
<i>Ceruttia sandiegoensis</i>	Calif. ^e		
“ <i>Miacis</i> ” <i>hookwayi</i>	Calif. ^{e,k}		
“Carnivoraformes Gen. B”	Calif. ^c	Calif. ^c	
<i>Lycophocyon hutchisoni</i>		Calif. ^f	
<i>Daphoenus lambei</i>			Tex. (cf.) ^b
<i>Daphoenus demilo</i> (= <i>D. lambei</i> ?)			Wyo. ⁿ , Sask. (cf.) ^h
<i>Daphoenictis</i> ? sp.			Tex. ^{b,s}
<i>Angelarctocyon australis</i>			N. Mex. (cf.) ^l , Tex. ^{b,u}
<i>Hesperocyon</i> sp.			Sask. ^h
<i>Nimravidae</i> indet.		Oreg. ^v	
<i>Eosictis avinoffi</i> (= <i>Brachyrhynchocyon</i> ? sp. ^b)			Utah ^{w,y}

Sources: ^aProthero (1996), ^bGustafson (1986), ^cFriscia and Rasmussen (2010; note Robinson et al., 2004, assigned the Chisos Formation, Texas, to Ui3), ^dWalsh (1996), ^eTomiya (2013), ^fWestgate (1990), ^gEaton (1985), ^hBryant (1992), ⁱStorer (1984), ^jEmry (1981), ^kStock (1934), ^lWesley and Flynn (2003), ^mPeterson (1919), ⁿDawson (1980), ^oTabrum et al. (1996), ^pStock (1935), ^qClark (1939), ^rTomiya (2011), ^sHunt (1996), ^tthis study, ^uTomiya and Tseng (2016), ^vHanson (1996), ^wScott (1945), ^xRasmussen et al. (1999), ^yKelly et al. (2012). Square brackets indicate occurrences for which voucher specimens are unknown to us. “Cf.” applies to taxonomic identification in original publication. Materials from southern California reported as “*Miocyon* cf. *M. scotti*” by Walsh (1996) are here considered *M. sp.* (cf. Tomiya, 2013), pending comparison with *M. vallisrubrae* (Friscia and Rasmussen, 2010). *Mimocyon longipes* Peterson, 1919 (listed as “*Miacis longipes*” in Gunnell et al., 2009) is likely a sinopanine hyaenodontid (cf. Dawson, 1980; Flynn and Galiano, 1982) and not included here.

~42 and 40 Ma, which culminated in the middle Eocene climatic optimum (Bohaty and Zachos, 2003; Doria et al., 2011 and references therein). The only ancient carnivoraform lineage that clearly survived beyond the Uintan was *Miocyon*. It is securely known from the Duchesnean of Saskatchewan, Canada, by an aberrantly large species *Miocyon magnus* (Bryant, 1992),

underscoring that taxa with more typical adaptations to the environmental conditions of the late Uintan were selected against during the Uintan–Duchesnean turnover event. Taken together, these observations suggest the possibility that the rise of crown-group carnivorans in North America was catalyzed by the late middle Eocene global climatic instability.

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LITERATURE CITED

- Bohaty, S. M., and J. C. Zachos. 2003. Significant Southern Ocean warming event in the late middle Eocene. *Geology* 31: 1017–1020.
- Bryant, H. N. 1992. The Carnivora of the Lac Pelletier Lower Fauna (Eocene: Duchesnean), Cypress Hills Formation, Saskatchewan. *Journal of Paleontology* 66: 847–855.
- Bryant, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Systematic Biology* 45: 174–189.
- Clark, J. 1939. *Miacis gracilis*, a new carnivore from the Uinta Eocene. *Annals of Carnegie Museum* 27: 349–370.
- Dawson, M. R. 1980. Paleontology and geology of the Badwater Creek area, central Wyoming: Part 20, the late Eocene Creodonta and Carnivora. *Annals of Carnegie Museum* 49: 79–91.
- Doria, G., D. L. Royer, A. P. Wolfe, A. Fox, J. A. Westgate, and D. J. Beerling. 2011. Declining atmospheric CO₂ during the late Middle Eocene climate transition. *American Journal of Science* 311: 63–75.
- Eaton, J. G. 1985. Paleontology and correlation of the Eocene Tepee Trail and Wiggins formations in the north fork of Owl Creek area, southeastern Absaroka Range, Hot Springs County, Wyoming. *Journal of Vertebrate Paleontology* 5: 345–370.
- Emry, R. J. 1981. Additions to the mammalian fauna of the type Duchesnean, with comments on the status of the Duchesnean "Age". *Journal of Paleontology* 55: 563–570.
- Figueirido, B., C. M. Janis, J. A. Pérez-Claros, M. De Renzi, and P. Palmqvist. 2012. Cenozoic climate change influences mammalian evolutionary dynamics. *Proceedings of the National Academy of Sciences of the United States of America* 109: 722–727.
- Flynn, J., J. Finarelli, and M. Spaulding. 2010. Phylogeny of the Carnivoramorph, and the use of the fossil record to enhance understanding of evolutionary transformations. Pp. 25–63 in: A. Goswami and A.R. Friscia, editors. *Carnivoran Evolution: New Views on Phylogeny, Form and Function*. Cambridge: Cambridge University Press.
- Flynn, J. J. 1998. Early Cenozoic Carnivora ("Miacoida"). Pp. 110–123 in: C. Janis, K. Scott, and L. Jacobs, editors. *Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. Cambridge: Cambridge University Press.
- Flynn, J. J., and H. Galiano. 1982. Phylogeny of early Tertiary Carnivora with a description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. *American Museum Novitates* 2725: 1–64.
- Friscia, A. R., and D. T. Rasmussen. 2010. Middle Eocene Carnivoramorph of the Uinta Basin, Utah. *Annals of Carnegie Museum* 79: 51–64.
- Gingerich, P. D. 1983. Systematics of early Eocene Miacidae (Mammalia, Carnivora) in the Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology (University of Michigan)* 26: 197–225.
- Gunnell, G. F., P. C. Murphey, R. K. Stucky, K. B. Townsend, P. Robinson, J. P. Zonneveld, W. S. Bartels, and L. B. Albright. 2009. Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American land mammal "ages". *Museum of Northern Arizona Bulletin* 65: 279–330.
- Gustafson, E. P. 1986. Carnivorous mammals of the late Eocene and early Oligocene of Trans-Pecos Texas. *Bulletin of the Texas Memorial Museum* 33: 1–66.
- Hanson, C. B. 1996. Stratigraphy and vertebrate faunas of the Bridgerian–Duchesnean Clarno Formation, north-central Oregon. Pp. 206–239 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge: Cambridge University Press.
- Heinrich, R. E., S. G. Strait, and P. Houde. 2008. Earliest Eocene Miacidae (Mammalia: Carnivora) from northwestern Wyoming. *Journal of Paleontology* 82: 154–162.
- Hunt, R.M., Jr. 1996. Amphicyonidae. Pp. 476–485 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge: Cambridge University Press.
- Kelly, T. S., P. C. Murphey, and S. L. Walsh. 2012. New records of small mammals from the middle Eocene Duchesne River Formation, Utah, and their implications for the Uintan–Duchesnean North American Land Mammal Age transition. *Paludicola* 8: 208–251.

- Lucas, S. G. 1982. *Vertebrate Paleontology, Stratigraphy, and Biostratigraphy of Eocene Galisteo Formation, North-Central New Mexico*. Authority of State of New Mexico.
- Lucas, S. G., and B. S. Kues. 1979. Vertebrate biostratigraphy of the Eocene Galisteo Formation, north-central New Mexico. Pp. 225–229 in: R. V. Ingersoll, L. A. Woodward, and H. L. James, editors. *New Mexico Geological Society Guidebook, 30th Field Conference*. Socorro, New Mexico: New Mexico Geological Society.
- Lyman, R. L. 2016. *Theodore E. White and the Development of Zooarchaeology in North America*. Lincoln, Nebraska: University of Nebraska Press.
- Peterson, O. A. 1919. Report upon the material discovered in the upper Eocene of the Uinta Basin by Earl Douglas in the years 1908–1909, and by O. A. Peterson in 1912. *Annals of Carnegie Museum* 12: 40–169.
- Prothero, D. R. 1994. The late Eocene–Oligocene extinctions. *Annual Review of Earth and Planetary Sciences* 22: 145–165.
- Prothero, D. R. 1996. Magnetic stratigraphy and biostratigraphy of the middle Eocene Uinta formation, Uinta Basin, Utah. Pp. 3–24 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge: Cambridge University Press.
- Prothero, D. R., and S. G. Lucas. 1996. Magnetic stratigraphy of the Duchesnean part of the Galisteo Formation, New Mexico. Pp. 199–205 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge: Cambridge University Press.
- Rasmussen, D. T., A. H. Hamblin, and A. R. Tabrum. 1999. The mammals of the Eocene Duchesne River Formation. Pp. 421–427 in: D. D. Gillette, editor. *Vertebrate Paleontology in Utah*. Salt Lake City, Utah: Utah Geological Survey.
- Robinson, P., G. F. Gunnell, S. L. Walsh, W. C. Clyde, J. E. Storer, R. K. Stucky, D. J. Froehlich, I. Ferrusquia-Villafranca, and M. C. McKenna. 2004. Wasatchian through Duchesnean biochronology. Pp. 106–155 in: M. O. Woodburne, editor. *Late Cretaceous and Cenozoic Mammals of North America*. New York: Columbia University Press.
- Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 8: 241–264.
- Scott, W. B. 1945. The Mammalia of the Duchesne River Oligocene. *Transactions of the American Philosophical Society* 34: 209–253.
- Solé, F., R. Smith, T. Coillot, E. De Bast, and T. Smith. 2014. Dental and tarsal anatomy of ‘*Miacis latouri*’ and a phylogenetic analysis of the earliest carnivoramorphs (Mammalia, Carnivoramorpha). *Journal of Vertebrate Paleontology* 34: 1–21.
- Solé, F., T. Smith, E. De Bast, V. Codrea, and E. Gheerbrant. 2016. New carnivoramorphs from the latest Paleocene of Europe and their bearing on the origin and radiation of Carnivoramorphs (Carnivoramorpha, Mammalia). *Journal of Vertebrate Paleontology* 36: e1082480.
- Stearns, C. E. 1943. The Galisteo Formation of north-central New Mexico. *Journal of Geology* 51: 301–319.
- Stock, C. 1934. New Creodonta from the Sespe Upper Eocene, California. *Proceedings of the National Academy of Sciences of the United States of America* 20: 423.
- Stock, C. 1935. *Plesiomiaceis*, a new creodont from the Sespe Upper Eocene, California. *Proceedings of the National Academy of Sciences of the United States of America* 21: 119.
- Storer, J. E. 1984. Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan), Saskatchewan. *Natural History Contributions (Museum of Natural History, Regina)* 7: 1–158.
- Tabrum, A. R., D. R. Prothero, D. Garcia, and R. J. Emry. 1996. Magnetostratigraphy and biostratigraphy of the Eocene–Oligocene transition, southwestern Montana. Pp. 278–311 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene Transition in North America*. Cambridge: Cambridge University Press.
- Thorpe, M. R. 1923. New species of Uinta Carnivora from White River, Utah. *American Journal of Science* 5: 218–224.
- Tomiya, S. 2011. A new basal caniform (Mammalia: Carnivora) from the middle Eocene of North America and remarks on the phylogeny of early carnivorans. *PLoS One* 6: e24146.
- Tomiya, S. 2013. New carnivoramorphs (Mammalia) from the middle Eocene of California, USA, and comments on the taxonomic status of ‘*Miacis gracilis*’. *Palaentologia Electronica* 16: 1–14.
- Tomiya, S., and Z. J. Tseng. 2016. Whence the beardogs? Reappraisal of the Middle to Late Eocene ‘*Miacis*’ from Texas, USA, and the origin of Amphicyonidae (Mammalia, Carnivora). *Royal Society Open Science* 3: 160518.
- Trouessart, E.-L. 1885. Catalogue des mammifères vivants et fossiles. Carnivores. *Bulletin de la Société d’Études Scientifiques d’Angers* 14 (Supplement to the year 1884): 1–108.
- U.S. Geological Survey National Center for EROS. 2005. Grayscale North America shaded relief (1-km resolution). Reston, Virginia: National Atlas

- of the United States. Available from: doi:10.5066/ F7DF6PQS
- Van Valen, L. 1966. Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History* 132: 1–126.
- Walsh, S. L. 1996. Middle Eocene mammal faunas of San Diego County, California. Pp. 74–119 in: D. R. Prothero and R. J. Emry, editors. *The Terrestrial Eocene–Oligocene transition in North America*. Cambridge: Cambridge University Press.
- Wang, X. 1994. Phylogenetic systematics of the Hesperocyoninae (Carnivora, Canidae). *Bulletin of the American Museum of Natural History* 221: 1–207.
- Wesley, G., and J. J. Flynn. 2003. A revision of *Tapocyon* (Carnivoramorpha), including analysis of the first cranial specimens and identification of a new species. *Journal of Paleontology* 77: 769–783.
- Westgate, J. W. 1990. Uintan land mammals (excluding rodents) from an estuarine facies of the Laredo Formation (middle Eocene, Claiborne Group) of Webb County, Texas. *Journal of Paleontology* 64: 454–468.
- Zack, S. P. 2019. A skeleton of a Uintan machaeroidine ‘creodont’ and the phylogeny of carnivorous eutherian mammals. *Journal of Systematic Palaeontology* 17: 653–689.